Architecture and growth strategy of two evergreen species of the Western Ghats (South India). Knema attenuata (Myristicaceae) and Vateria indica (Dipterocarpaceae)

Muriel Durand

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OF TWO EVERGREEN SPECIES

OF THE WESTERN GHATS (SOUTH INDIA)

KNEMA ATTENUATA (MYRISTICACEAE)

AND *VATERIA INDICA* (DIPTEROCARPACEAE)

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Abstract

Analysing tree architecture consists in describing the successive growth stages from the seedling to the death of plants. The description and monitoring of the different types of axes (stem, branches, twigs, *etc.)* and lateral productions (flowers, leaves, *etc.)* helps in characterising the structural growth strategies.

In this paper, I describe and interpret the architectural development of two species: *Vateria indica* (Dipterocarpaceae), an emergent, and *Knema attenuata* (Myristicaceae), a lower canopy species. These two species are among the most frequent species of the low elevation moist evergreen forests of the Western Ghats in South India. They were observed in the Kadamakal Reserve Forest (Coorg District, Karnataka State).

Both species conform to Massart's architectural model but exhibit different ways of building up their crown and different strategies of reiteration in response to light availability in order to maintain their growth under canopy: *K. attenuata* reinforces its structure from the very early stage and maintains its position of a lower canopy tree through its very regular structure until it reaches the canopy, while *V. indica* establishes its structure once it reaches this limit.

The aim of this paper is to show how two species which belong to two different vertical strata, grow and adapt in the light-limited forest environment and to describe by which way they manage to reach the canopy and intercept light.

Key words: rain forest, tree architecture, forest dynamics, silvigenesis, metamorphosis, growth strategy.

Résumé

L'analyse architecturale des plantes est une discipline récente basée sur la description des stades successifs de la croissance, de la plantule jusqu'à la sénescence. Par la caractérisation des différents types d'axes (tronc, branches, rameaux, *etc.)* et de productions latérales (fleurs, feuilles, *etc.),* elle permet, entre autres, de mettre en évidence les stratégies de croissance des arbres.

Dans cet article, je décris et interprète l'architecture de deux espèces : *Vateria indica* (Dipterocarpaceae), émergent, et *Knema attenuata* (Myristicaceae), arbre atteignant la canopée. Ces deux espèces sont parmi les plus fréquentes des forêts denses humides sempervirentes de basse altitude des Ghats occidentaux du Sud de l'Inde. Elles ont été observées dans la Forêt de Kadamakal (district du Coorg, état du Karnataka).

Bien que ces deux espèces soient toutes deux conformes au modèle de Massart dans leurs jeunes stades, leur stratégie de croissance est différente en ce qui concerne l'édification du tronc, l'extension de la couronne par réitération et la réaction aux conditions lumineuses : *K. attenuata* investit et renforce sa structure dès les plus jeunes stades avant d'atteindre la canopée, alors que *V. indica* ne s'épanouit qu'une fois cette limite atteinte.

Cet article montre comment croissent deux espèces de statut social différent dans un milieu contraignant et quels sont les moyens structurels qu'elles utilisent pour atteindre la canopée et intercepter la lumière.

Mots-clés : forêt dense, architecture des arbres, dynamique forestière, sylvigenèse, metamorphose, stratégie de croissance.

Introduction

This working paper presents an architectural study of two species which are present in the low elevation moist evergreen forests of the Western Ghats in South India: *Vateria indica* and *Knema attenuata*[1]. This work is part of a project of the French Institute of Pondicherry (Houllier *et al.* 1997) whose long term objective is to model and simulate the dynamics and functioning of these forests.

The study of tree architecture was initiated by Corner (1949, 1953, 1954), followed by the syntheses of Hallé & Oldeman (1970) and Hallé *et al.* (1978) with the notion of architectural models. Since then, several studies have been carried out in tropical regions. Among the most recent ones we may cite: Barthélémy (1988), Sanoja (1992), Drenou (1994), Loup (1994) and Loubry (1994) in South America; Edelin (1984) and Barthélémy (1988) in South-East Asia. Some species of Dipterocarpaceae were studied in Malaysia by Hallé (1979), Hallé & Khamil (1981), Hallé & Ng (1981) and Edelin (1984), the latter describing the phenomenon of architectural metamorphosis. Architectural analyses of some Myristicaceae species have also been carried out (Loubry 1994, Drenou 1994). Although these studies mostly concern the architecture of the above-ground part, the root system has also been studied by Atger (1992) and Jourdan (1995).

The aim of this paper is to characterise (*i*) the architecture and successive growth stages of the two above cited species based on their morphological characters, and *(ii)* the structural growth strategies of these species *(i.e.*, the way they reach the canopy and intercept light).

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[1] This study is part of a doctoral thesis.

Materials and methods

This study was carried out in a permanent station monitored by the French Institute near Uppangala (Kadamakal Reserve Forest, Coorg District, Kamataka). Since 1985, several studies have been conducted in this station, especially on the forest structure and silvigenesis (Loffeier 1988, Pascal & Pélissier 1996, Pélissier 1995, Elouard *et al.* 1997). This forest has a high species diversity (about 65 species per hectare), but only 4 to 6 species represent more than 50% of the trees and basal area (Pascal & Pélissier 1996). Here we study the architectural development of two of the most common species, *viz., Vateria indica* (Dipterocarpaceae) and *Knema attenuata* (Myristicaceae).

Vateria indica is the second most frequent species and is an emergent or upper canopy species, which can attain a height of 45 m. *Knema attenuata* is a lower canopy species, which can grow up to 25-30 m. Although slightly less frequent than another Myristicaceae, *Myristica dactyloides, K. attenuata* was finally selected for this study, because its architecture and ecology are approximately similar to that of *M. dactyloides* and because early architectural stages of *M. dactyloides* were very rare. The lack of seedlings and saplings of the latter species is probably due to the regular collection of fruits by villagers over about thirty years (arils are used for dyeing).

The architectural analysis of a tree is based on the morphological description of all its axes at different growth stages. Hence, all the principal structural forms exhibited by the plant from the seedling stage to its death can be deduced from field observations. Only the above-ground part of the plant is considered. From the comparison of different trees at various stages, one of the first steps in architectural analysis is to define the **architectural unit** of the species (Edelin 1977, Barthélémy *et al.* 1989), which represents the specific structure expressing the maximum level of hierarchical differentiation. The architectural unit shows the different axes that can be identified and characterised by various criteria (morphological, quantitative and qualitative). For instance, the architectural unit of *Platanus hybrida* described by Caraglio and Edelin (1990) is composed of one trunk, branches (A2), twigs (A3), branchlets (A4) and small branchlets (A5). These results are usually presented in a descriptive table.

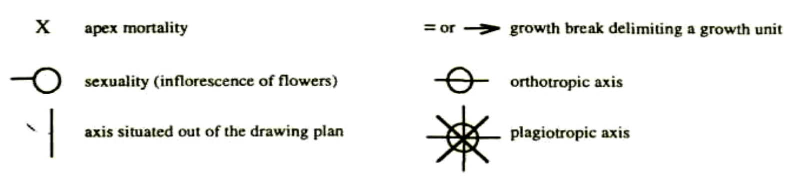
This architectural unit can then be duplicated: this is the **reiteration** phenomenon (Oldeman 1974, Edelin 1986, Barthélémy *et al.* 1991), which is often associated with the set-up of the main branches and the expansion of the tree crown, which gradually becomes a polyarchic structure (Edelin 1991) organized around the main axis. With age, the replication of the architectural unit, whether partial or total, becomes poorer and poorer until only the minimal architectural unit is replicated (Barthélémy 1988, Drenou 1994).

Several criteria need to be considered while analysing the architecture:

- *Growth type.* Growth may be **rhythmic** when there is alternation of resting and growing periods. All the structures established during the same active extension period correspond to a growth unit (GU of Hallé & Martin 1968, Comte 1993). Or growth may be **continuous,** *i.e.*, without a resting period.
- *Direction of growth.* Growth may be **vertical** or **horizontal.** Generally, the symmetry is associated with the direction of growth and an axis is defined as **plagiotropic** if it has a bilateral symmetry and grows horizontally. This is generally expressed by a distichous phyllotaxy and a dorso-ventral axis. An axis is called **orthotropic** if its growth is oblique to vertical and if it has a radial symmetry and, generally, exhibits a spiral phyllotaxy. An intermediate case, **mixed** axis, may be found when the axis has a basal vertical part in the role of trunk and a distal horizontal part in the role of a branch, separated by a curve of variable radius in the role of top (Hallé & Oldeman 1970).
- *Branching type.* Branching may be **terminal** or **lateral** but for most of the plants branching is lateral. In the latter case it may be **monopodial** when branching results from the indeterminate growth of the apical meristem, or **sympodial** when it results from the determinated growth of successive meristems. Branching is said to be **continuous** if all the leaf axils show branches, **diffuse** if its branches are irregularly spaced, and **rhythmic** if this spacing is regular. When the lateral meristem is formed, it may grow either without any resting period in a synchronous growth or after a resting period. We then speak of branches with **immediate** (sylleptic) or **deferred** (proleptic) growth.
- *Position of sexuality.* Flowering may be **terminal** or **lateral** on the axis.

Drawing is the basis of architectural analysis; it is a means of representation and at the same time a way of observing the plant. Growth patterns can be hypothesised by comparing the drawings of trees at different stages and in different conditions.

In the drawings (Plate 1 to 14), the following signs are used to represent different functions and structures:



Field observations were made with the help of Leitz (10x50) binoculars and Kowa TSN-1 (x60) telescope. Trees were observed and drawn in the permanent plots themselves or in their vicinity with the aim to cover the complete life cycle of the two species.

Growth monitoring is a valuable but time-consuming technique for it provides a diachronic approach of tree development but requires to precisely locate the trees and tag the various branches. In this study, one-year monitoring *(i.e.,* two observations at a one-year interval) was carried out on younger trees (1-5 m height) situated in different light conditions (see Houllier *et al.* 1997).

Results

Vateria indica L. (Dipterocarpaceae)

The seedling

On germination, the seedling puts forth an epigeal shoot (Al) with orthotropic, monopodial and rhythmic growth (Pl. 1.1). The first two or four leaves are opposite and decussate. The tip of the plant has a bunch of simple, entire, oval, acuminate leaves whose secondary veins are curved near the leaf margin. There is a bulge in the proximal part of the petiole, just before the lamina, called pulvinus. The leaves are arranged along a spiral with a 2/5 phyllotaxy. The root system is a tap root with a few lateral roots.

The young sapling

The young plant (Pl. 1.2) produces a succession of growth units (GU) on the trunk which are sometimes difficult to determine. They can, however, be identified (Pl. 1.3) by the presence of solitary stipules ("scales") at the first nodes, and then by the two stipules surrounding an aborted leaf. These stipules are caducous and separated by short internodes. The upper part of the GU has well developed leaves which, on falling, leave distinct ovoid leaf scars. These leaves are generally separated by longer internodes. A few aborted leaves may appear after the developed ones just before the bud. Sometimes the shoot elongates very slowly and the leaves are unable to spread out, resulting in a series of "scales" (stipules) or aborted leaves.

Branching of the sapling

Vateria indica gradually produces a monopodial, orthotropic **trunk** (Al) (Pl. 1.4). It sometimes exhibits apical mortality depending on the growth conditions and its location in the forest (Durand *et al.* 1995). After putting forth several GUs, the young plant produces branches with immediate growth (sylleptic) in the middle part of the GU from nodes bearing aborted or developed leaves (Pl. 1.5). This branching is rhythmic.

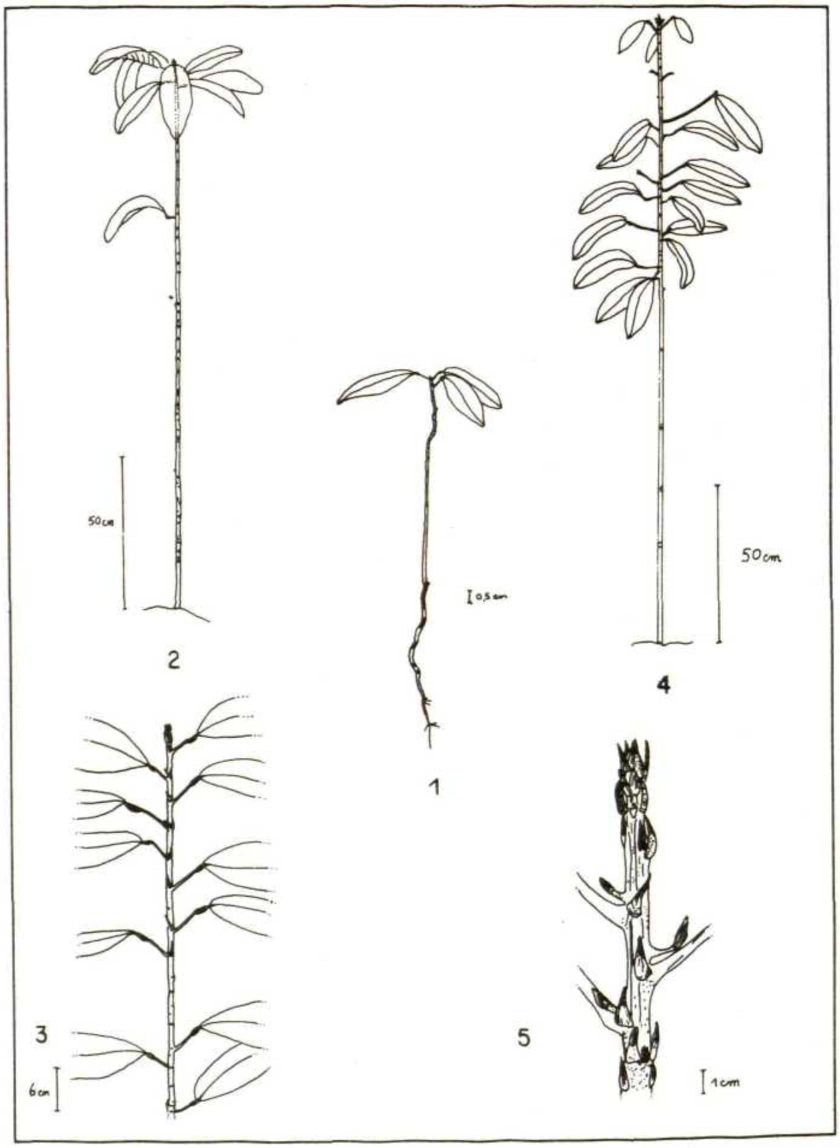


Plate 1. *Vateria indica:* **1** - Seedling; **2** - Unbranched sapling; **3** - Growth unit; **4** - Branched sapling; **5** - New flush with sylleptic branches.

The **branches** (A2) thus formed are horizontal, most often monopodial, and exhibit rhythmic growth. The prophylls, and sometimes the first leaves, of these lateral branches are alternate and distichous, while the later leaves show spiral phyllotaxy. The leaves tend to be arranged horizontally by a twisting of the pulvinus, thus exhibiting secondary distichous phyllotaxy. The axis then appears to be plagiotropic.

Whatever the type of axis, the leaves are generally persistent on three of the last four GUs produced.

Establishment of the architectural unit

At first, the young tree shows widely spaced levels of branches (A2) and generally exhibits monopodial growth and rhythmic branching. These **twigs** (A3) show immediate growth in the middle of the GU, spiral 2/5 phyllotaxis and are secondarily plagiotropic. The crown represents about two third of the tree height (Pl. 2).

Little by little, the lowest branches get self-pruned. They are horizontal and very often their apical meristem dies. They produce small, vertical, orthotropic lateral shoots with deferred growth, but these are short lived. These **small orthotropic structures** (Pl. 3.1) are rarely branched and are found in the apical to middle part of the GU, on nodes with mature leaves. These structures are also found on older trees.

In the middle part of the crown, the branches (A2) are secondarily plagiotropic and tend to straighten up at their apical part. The twigs are plagiotropic. The branches seem denuded because of the presence of leaves in only the apical part, generally on the last two or three youngest GUs. This phenomenon is emphasised by the rapid self-pruning of the twigs situated at the basal part of the branch. The well developed branches show increasingly frequent apical mortality. Two or three "relays"[2] then develop below the dead apices. When three "relays" develop (Pl. 3.2 a & b), two of them are at the same level and the third is above and parallel to the other two. In the upper part of the tree, the growth of the branches becomes increasingly oblique with some of them ultimately becoming orthotropic (Pl. 3.3).

[2] A "relay" is a lateral axis which becomes dominant after the death of its main carrier axis.

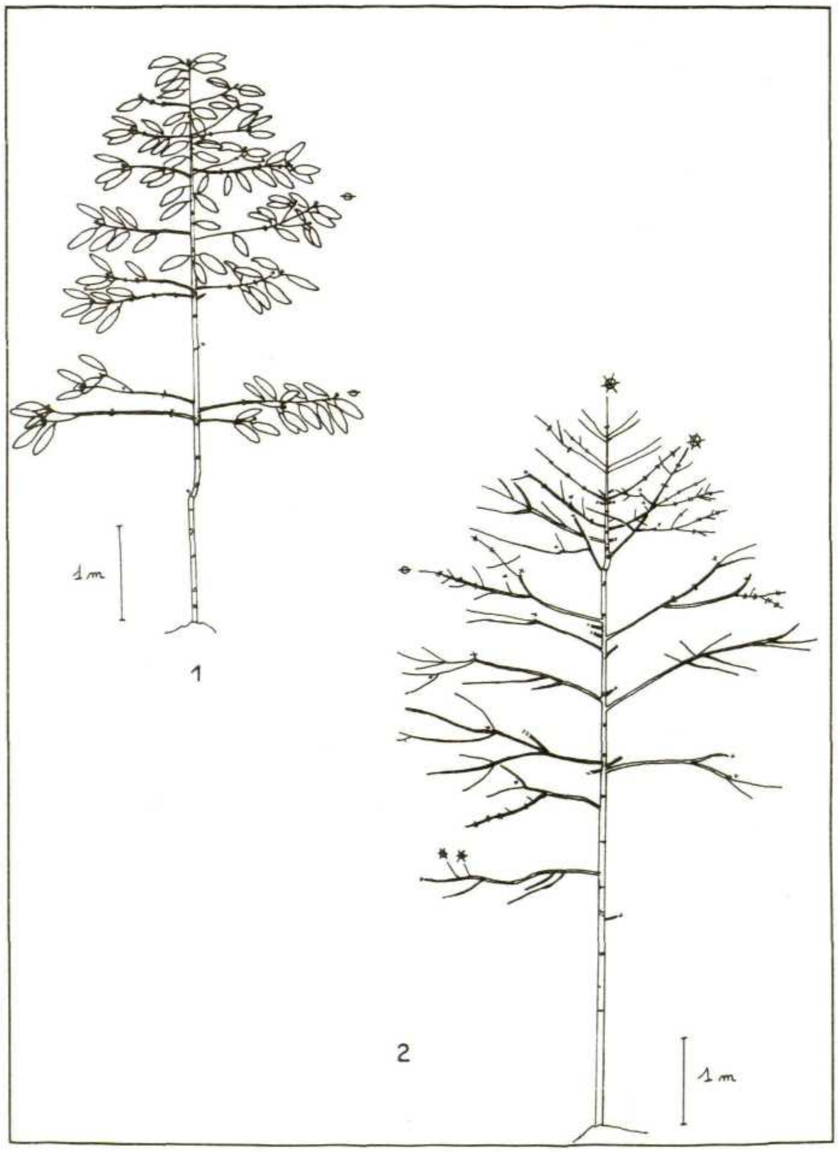


Plate 2. *Valeria indica:* 1 - Young tree expressing its architectural unit; 2 - Expression of branching. Note the presence of the orthotropic structure on the lower branch.

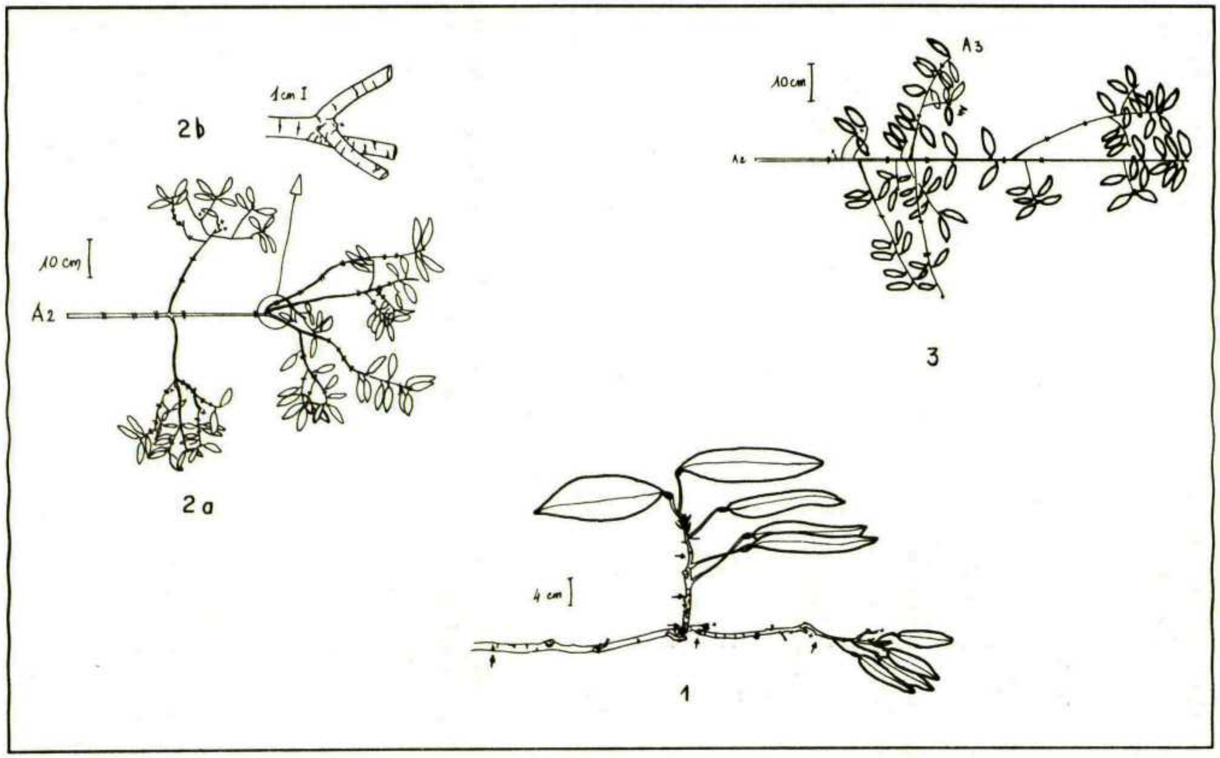


Plate 3. *Vateria indica*: **1** - Small orthotropic structure; **2a** - Branch (A2) of a young tree ; **2b** - Detail of the "relays"; **3** - Orthotropic branch.

At this stage, the young plant conforms to Massart's architectural model. It has therefore attained its architectural unit. The characteristics of the architectural unit are summarised in Table 1.

Table 1. Recapitulative table of the architectural unit of *Vateria indica.*

<table>
<tr><th></th><th></th><th colspan="2">Trunk – Axis 1</th><th colspan="2">Branches – Axis 2</th><th colspan="2">Twigs -Axis 3</th></tr>
<tr><td rowspan="5">Primary growth</td><td>type</td><td colspan="6">rhythmic</td></tr>
<tr><td>primary direction</td><td colspan="3">orthotropic</td><td colspan="3">secondarily plagiotropic</td></tr>
<tr><td>secondary direction</td><td colspan="3">vertical</td><td colspan="3">horizontal</td></tr>
<tr><td>life span</td><td colspan="3">long</td><td colspan="3">moderate</td></tr>
<tr><td>symmetry</td><td colspan="3">radial</td><td colspan="3">bilateral</td></tr>
<tr><td>Structure of the GU</td><td>markers of cessation of growth</td><td colspan="6">short internodes and scales</td></tr>
<tr><td rowspan="2">Branching</td><td>type</td><td colspan="6">rhythmic</td></tr>
<tr><td>chronology</td><td colspan="6">immediate</td></tr>
<tr><td>Leaves</td><td>phyllotaxy</td><td colspan="6">spiral with 2/5 phyllotaxy</td></tr>
<tr><td>Flowering</td><td>type</td><td colspan="6">sterile</td></tr>
</table>

Metamorphosis

The lowest branches of the crown are most often in the shade (Pl. 5.1). They bear long plagiotropic hanging twigs (A3), whose apex is often dead. Some of these branches exhibit a succession of dead apical meristems and "relays", giving rise to forks. In the long term the lowest branches die and eventually get self-pruned when the apical meristem dies, the lower branches with 3 relays begin to grow (Pl. 3.2). The relay situated above the others is thicker, its growth is mostly monopodial and its apical part changes its direction (becoming oblique). The relays become orthotropic, the leaves and twigs are arranged radially on the branch. These relays are generally in the light, the others retaining the characteristics of plagiotropic branches (horizontal and monopodial growth).

Sometimes the lowest branches get broken although they have a large girth: in their middle part, structures similar to young trees can then be observed. These structures correspond to total reiteration complexes replicating the young tree (orthotropic trunk and plagiotropic branches) or to a vertical reiteration of the basic structure (all orthotropic axes), the latter being more frequent on the branches (Pl. 4.1).

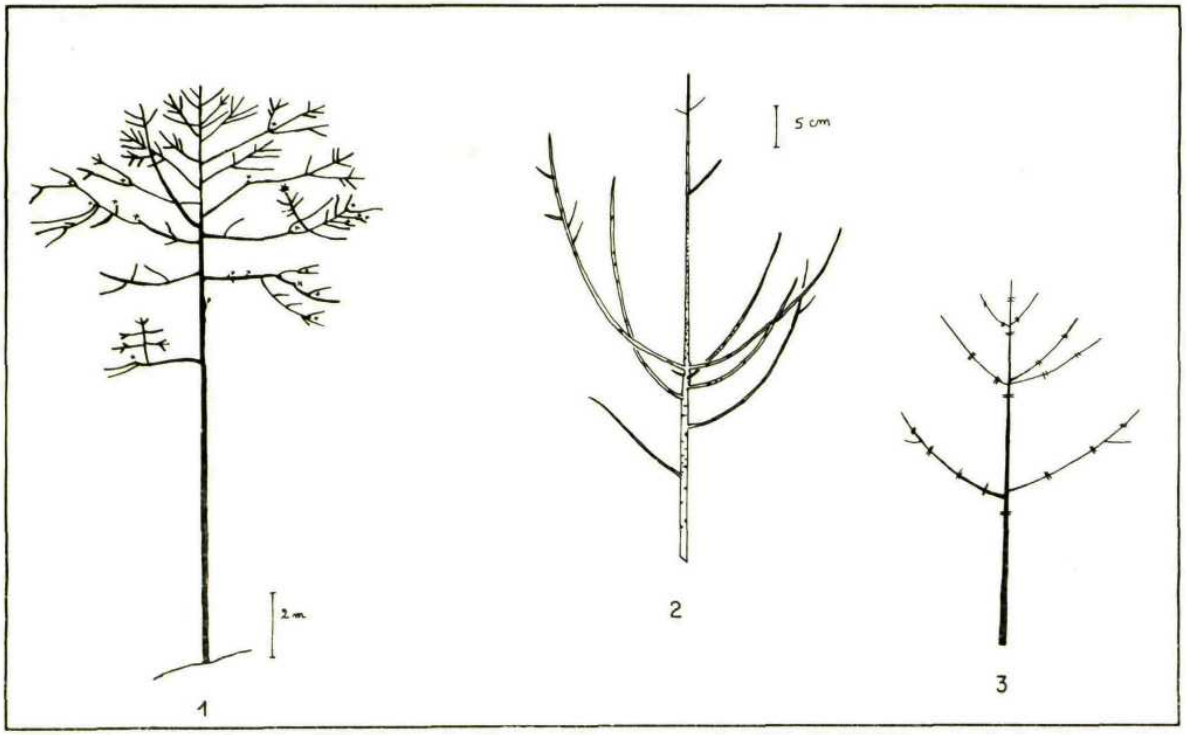


Plate 4. *Vateria indica*: **1** - Tree metamorphosis; **2** - Drawing of the basic structure; **3** - Diagram of the basic structure.

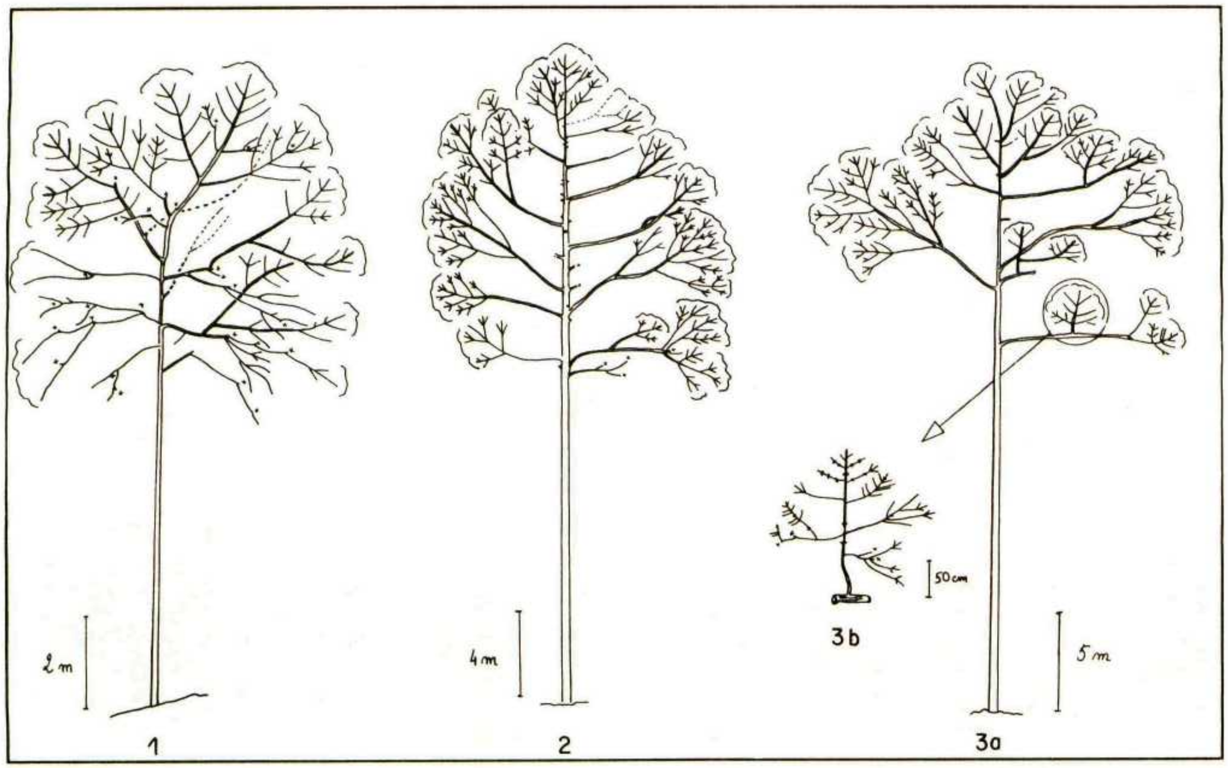


Plate 5. *Vateria indica*: **1** - Beginning of the metamorphosis; **2** - Metamorphosis on all the branches; **3** - Appearance of total reiteration.

The biggest branches in the centre of the crown are modified (Pl. 4.1). Their direction of growth becomes oblique and all the axes become orthotropic. Phyllotaxy is spiral, the leaves are radially arranged around the branch and the pulvinus get "untwisted". The orthotropy appears on the apical part of the branch, extending to the whole branch. Each type of axis is then orthotropic (trunk, branches and twigs). In this paper, this structure is called the **basic structure of metamorphosis** (Pl. 4.2 & 4.3). The twigs (A3) quickly bear one or two supplementary orders of branching, replicating the basic structure described above. Hence, numerous reiterated complexes can be observed. Some are sylleptic, formed by the apical meristems of growing axes by direct and progressive transformation of the axes (metamorphosis), and some are proleptic formed by latent meristems. These phenomena help the branch to spread. During metamorphosis, a part of the crown is exposed to light.

In the uppermost part of the crown, the branches are inserted in a more acute angle, their growth becomes increasingly oblique and they are wholly orthotropic. In fact, the arrangement of the twigs becomes radial, at first in the middle of the branch, and later from the base of the branch.

At this stage, the tree undergoes real **metamorphosis** (Edelin 1984) of its branches throughout the crown, producing numerous sylleptic reiterations. This phenomenon appears when the tree reaches the upper canopy and the crown is in full light. A few wholly proleptic vertical reiterations are sometimes observed on the middle part of branches.

Expansion of the crown

When the tree reaches the canopy, most of its crown is exposed to light. Metamorphosis takes place in every axes (Pl. 5.2). All the branches are orthotropic and bear sylleptic and proleptic reiterations. Every main branch is then composed of a reiterated complex group forming a crownlet. Several crownlets together form the crown of the tree. On the lower branches, when branches get broken, a few vertical and total orthotropic reiterated complexes (Pl. 5.3) are produced.

Thus, the formation of these reiterated complexes allows the tree to expand its crown which had remained small during its earlier stages of growth, due to the small number of twigs (A3) that *Vateria indica* produced. The size of the crown depends on the available space.

The adult tree: flowering

It is only after the most branches are metamorphosed that the lateral inflorescences are observed on some basic structures (Pl.. 6).

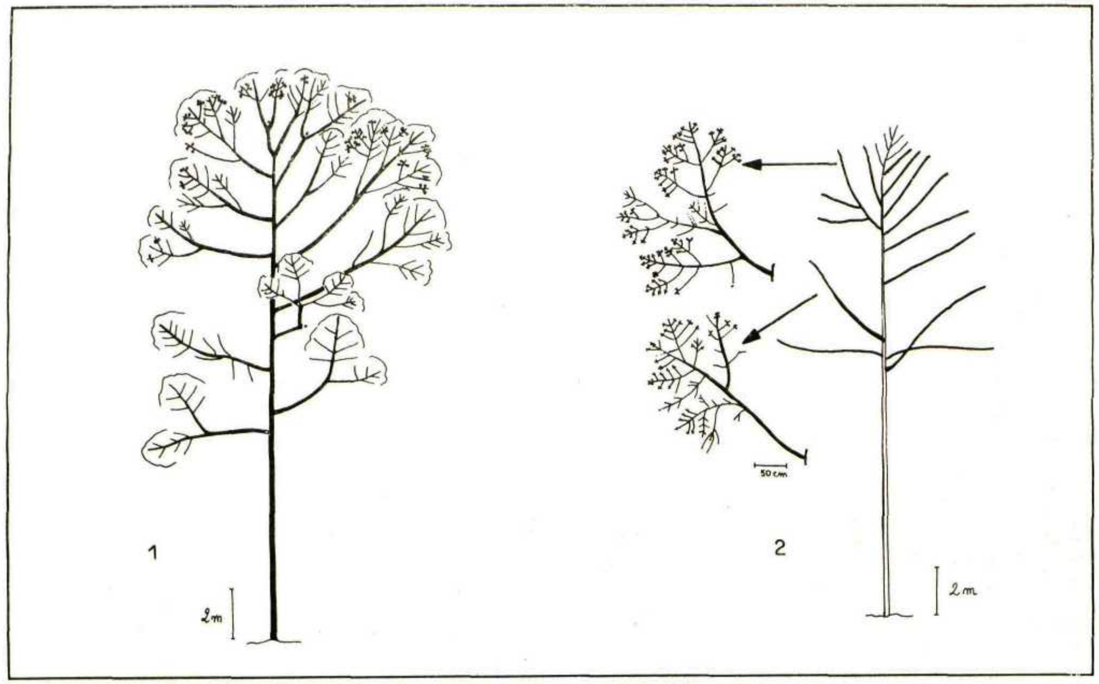


Plate 6. *Vateria indica*: **1** - Expression of flowering; **2** - Position of the inflorescences.

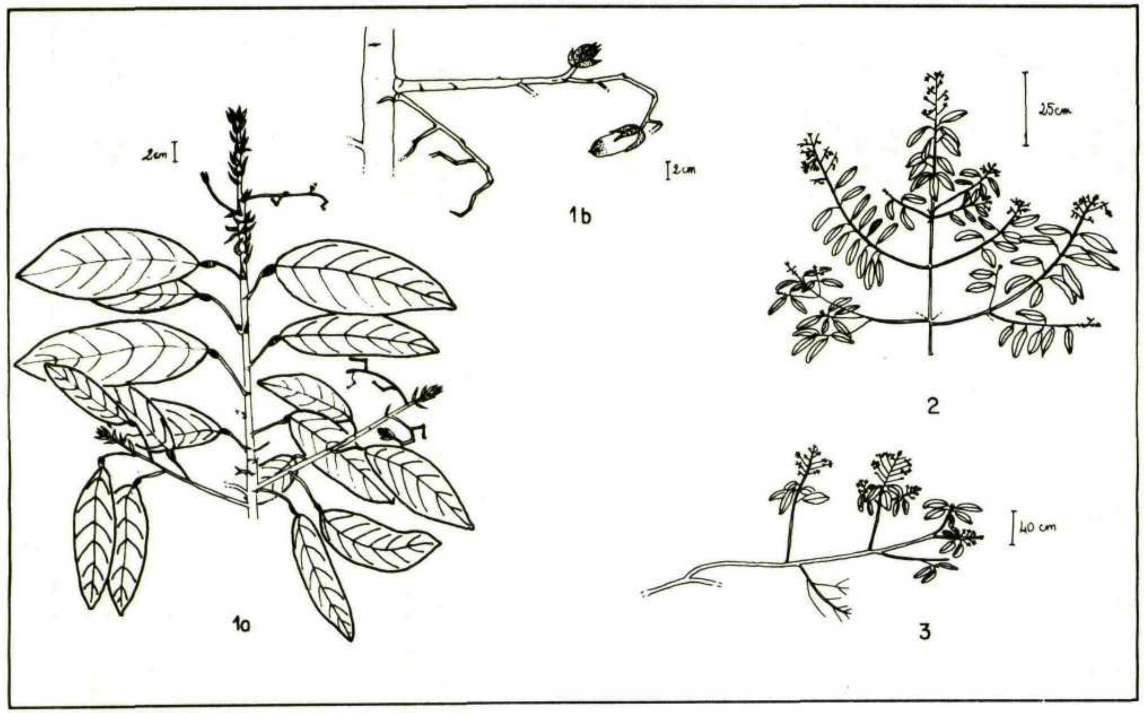


Plate 7. *Vateria indica*: **1a** - Flowering axis; **1b** - Double flowering axis; **2** - Flowering gradient; **3** - Epitone flowering axis.

The inflorescences (Pl. 7.1a) are open clusters (basifugal blooming). The flowering axes are lateral and appear in the middle part of the GUs. After the monsoon, some trees have a vegetative elongation phase when they produce smaller, waffled, thicker leaves which are more oblong in shape. Another period of elongation follows producing a series of stipules (17-18 nodes). Flowering axes are produced from the axils of most of these nodes. At the tip of the main axis there is a bud made up of leaf primordia and large stipules.

Fruits are dry, green, ovoid, tomentose and barochorous (Pl. 7.1b). Therefore, young *Vateria indica* trees are often grouped together near an adult tree.

At first, the inflorescences are found on the bigger branches of the crown top, in the apical part of all the axes of the new reiterated complexes (Pl. 6.1) in such a way that all the flowers are found at the periphery of the crown. When the majority of branches are to blossom, the tree is completely covered by a coat of white flowers. Flowering does not stop the vegetative growth of the tree; the main apices remain active even after lateral flowering.

All the axes of the basic structure flower, but we can observe a gradual expression of flowering within the architecture (Pl. 7.2). Flowering is more frequent in the uppermost axis. Therefore, every reiteration produces the **flowering basic structure** (summarised in Table 2). The inflorescences are sometimes positioned on vertical young axes, corresponding to proleptic reiterations appearing in an epitone way on the branches (Pl. 7.3).

Table 2. Recapitulative table of the structure established at the time of metamorphosis.

		Trunk- Axis 1	**Branches-** Axis 2	**Twigs-** Axis 3
Primary growth	type	rhythmic		
	primary direction	orthotropic		
	secondary direction	oblique to vertical		horizontal to oblique
	symmetry	radial		
Structure of the GU	marker of cessation of growth	Short internodes and scales		
Branching	type	rhythmic		unbranched
	chronology	immediate		unbranched
Leaves	phyllotaxis	spiral with 2/5 phyllotaxis		
Flowering	type	fertile		
	location	lateral		

Although flowering does not hinder the growth of the tree, it is nevertheless correlated with a subsequent decrease of the size of the growth units and of the life span of the reiterated complexes, thus leading the tree towards senescence.

The tree of the past: senescence

On ageing, most main branches of *Vateria indica* get broken and a succession of reiterations can be observed (Pl. 8.1 & 3). Their life span becomes shorter and shorter. As before, reiteration duplicates the flowering basic structure. In any case, the older the tree, the more the reiterated structures get simplified (Pl. 8.2). Thus, there is a reduction in the size of the growth units and the different types of branches gradually disappear.

The structure that was characterised by three types of flowering axes (trunk, branch, twigs) now becomes a structure with only one flowering axis (trunk) which seems to be the minimum architectural unit of reiteration (Barthélémy 1988, Drenou 1994). Total proleptic reiterations can also appear on the main branches (Pl. 8.3). However, this is a rare phenomenon, which is found mostly on the lowermost branches of the crown. Such branches are denuded in their basal part.

Summary of the architectural development

First, *Vateria indica* puts forth one orthotropic stem composed of a succession of GUs (Pl. 9.1) and only a few leaves remain on the top. Then a few branches grow (Pl. 9.2) with leaves arranged spirally with a 2/5 phyllotaxy. These branches are horizontal and are secondary plagiotropic. *Vateria indica* conforms to Massart's model. Later the plant puts forth some twigs and expresses its architectural unit (Pl. 9.3). Some small orthotropic structures appear on the lower branches.

Once all these axes have appeared, the main axis starts its metamorphosis, the main branches change their direction and all the axes become orthotropic (Pl. 9.4). The tree expresses a new structure, the basic structure of metamorphosis. This phenomenon appears when the tree reaches the canopy, receives more light and has enough space to expand its crown.

Once all the branches are metamorphosed, the tree flowers (Pl. 9.5) at the periphery of the crown. Then the tree becomes senescent (Pl. 9.6): the basic structure gets reduced; the growth unit decreases and branching disappears gradually. The tree of the past expresses only its minimum unit of reiteration.

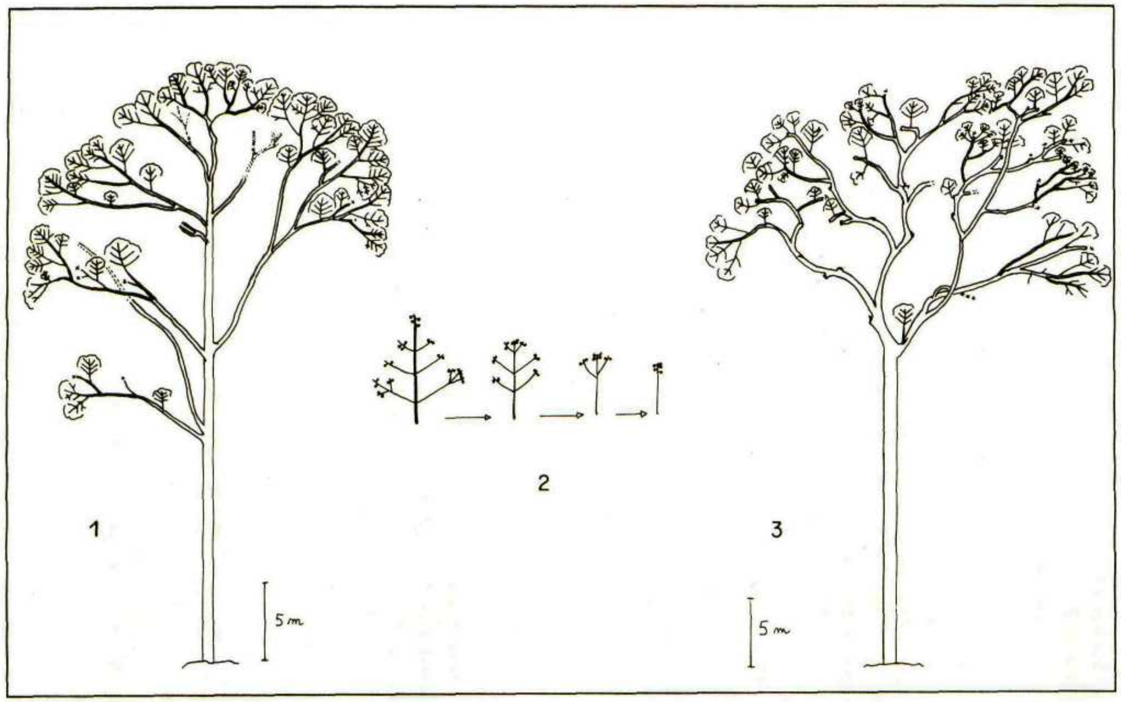
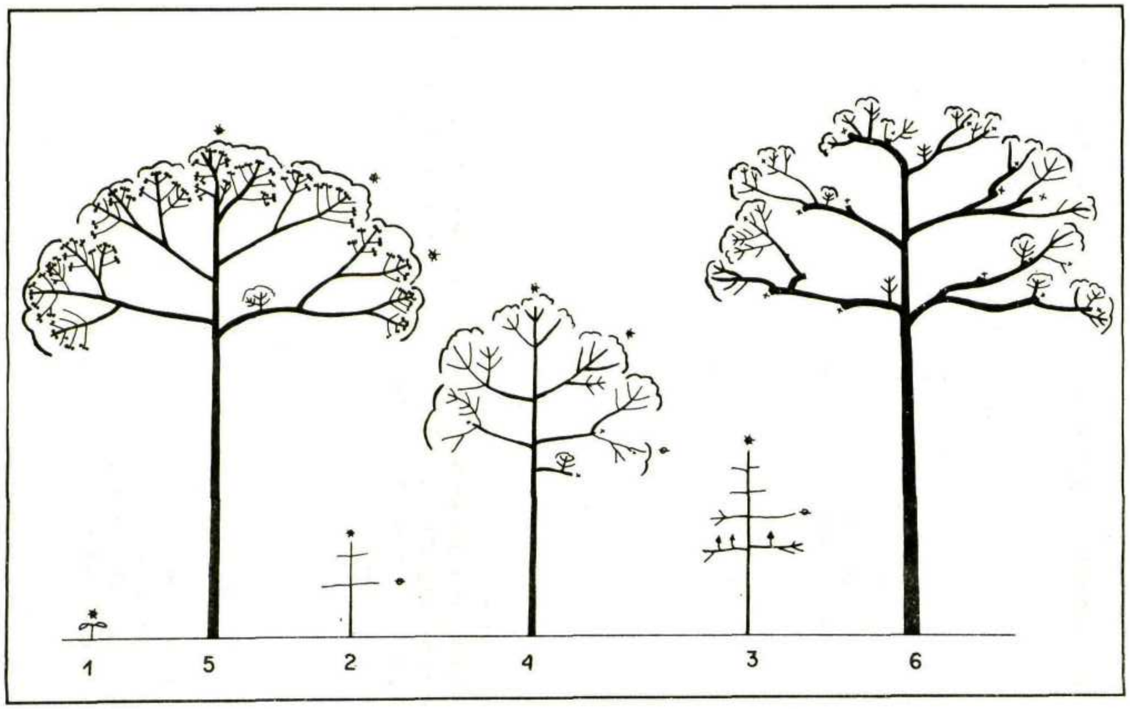


Plate 8. *Vateria indica*: **1** - Adult tree; **2** - Evolution of the basic structure; **3** - Old tree.



Piate 9. *Vateria indica*: scheme of development.

Knema attenuata (J. Hk. & Thw.) Warb (Myristicaceae)

The seedling

On germination the seedlings (Pl. 10.1) have an orthotropic monopodial axis with rhythmic growth, producing a succession of deciduous leaves in the lower part, and of persistent leaves in the upper part. The leaves are alternate, spirally arranged in a 2/5 phyllotaxis, simple, entire and acuminate. The first internodes are quite long while subsequent nodes become shorter before the cessation of growth. Branches appear at the level of the last internodes. Thank to growth monitoring, the first nodes corresponding to prophylls *a* and *b* were observed to be short indicating a resting period.

Each growth unit (Pl. 10.2) is thus characterised by a basal leafless and unbranched part with longer internodes and an apical part with shorter internodes, persistent leaves and branches (about 4-5) forming a "pseudowhorl". The GU ends with a few short internodes and undeveloped lamina. In the younger stages, the branches are short lived (one or two growth flushes only).

The young sapling

The young plant (Pl. 11.1), made up of a succession of growth units as described above, has an orthotropic **trunk** with monopodial growth and rhythmic branching. The **branches** are plagiotropic, exhibit horizontal growth and are inserted radially on the trunk. Leaves are alternate with distichous phyllotaxy and arranged in a horizontal plane. Because of their short life span, there are only 3-5 layers on the tree. The lowermost branches tend to have only one growth flush and then die. Limits of the GUs are not evident on the branches, because a small leaf or an aborted leaf scar is their only morphological trace.

From the point of view of elongation dynamics, branches show more flushes than the trunk: they have a different growth rhythm. After the last monsoon rains (Nov.- Dec. 1995), in some individuals, only the branches grew, while the trunk did not, while in others the trunk and branches grew together.

Branching is diffuse. The **twigs** (A3) are small, solitary or coupled and show deferred growth. These twigs with monopodial growth gradually become longer. *Knema attenuata* conforms to Massart's model.

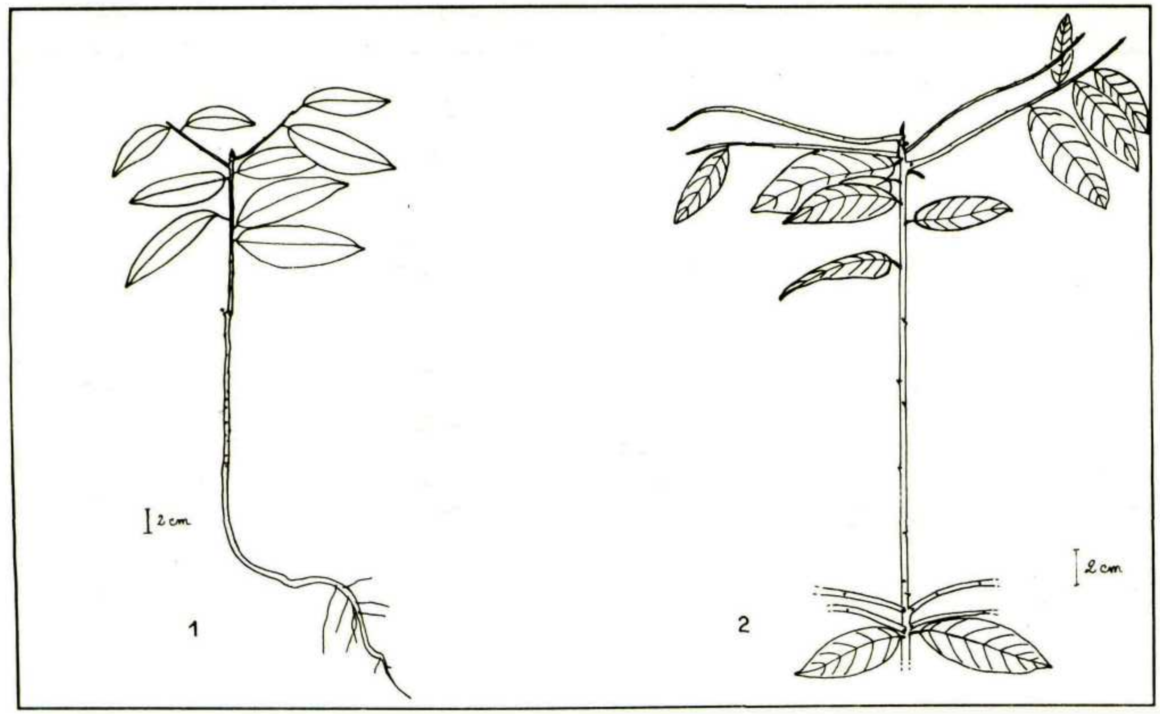


Plate 10. *Knema attenuata*: **1** - Seedling; **2** - Growth unit.

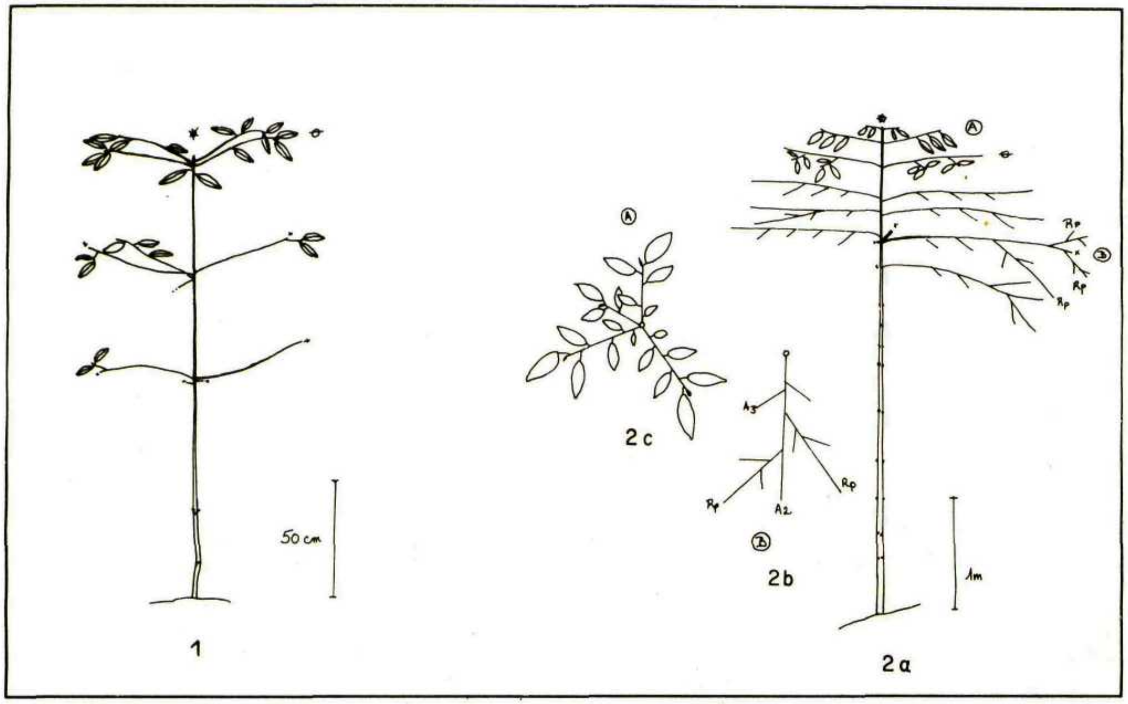


Plate 11. *Knema attenuata*: **1** - Sapling; **2a** - Branching on sapling; **2b** - Lower branch (top view); **2c** - Upper branch (top view).

Branching

At this stage (Pl. 11.2), the trunk shows very regular levels of branches (pseudowhorls) which may be quite long. On these stems the branching becomes rhythmic. The twigs are long, especially the lowermost ones which occupy the maximum space. They also branch in a diffuse manner, but the **branchlets** (A4) are rare. The branch diameter is small compared to the trunk. The crown is compact due to numerous branches (4-6 per pseudowhorl), non-aligned twigs and the large number of levels as compared to the height of the crown (6-10 layers over a height of about 5 m).

Establishment of the architectural unit

At this stage, the trees have not yet reached the canopy and *Knema attenuata* is characterised by the high regularity of its structure. The crown is dense and spreads by the elongation of branches and twigs. The large branches in the middle of the crown (**Pl. 12**) produce short bifid flowering axes. They first appear on the twigs and then spread to the branchlets and along the branches. These **spurs** have an immediate growth.

Hence, when the tree reaches a height of about 15 m, branching is fully expressed and the tree begins to flower. It has therefore attained its architectural unit (summarised in Table 3).

Table 3. Recapitulative table of the architectural unit of *Knema attenuata.*

<table>
<tr><th colspan="2"></th><th>Trunk
Axis 1</th><th>Branches
Axis 2</th><th>Twigs
Axis 3</th><th>Branchlets
Axis 4</th><th>Spurs - Short flowering axis</th></tr>
<tr><td rowspan="4">Primary growth</td><td>type</td><td colspan="5">rhythmic</td></tr>
<tr><td>primary direction</td><td>orthotropic</td><td colspan="3">plagiotropic</td><td>—</td></tr>
<tr><td>secondary direction</td><td>vertical</td><td colspan="4">horizontal</td></tr>
<tr><td>symmetry</td><td>axial</td><td colspan="3">bilateral</td><td>axial</td></tr>
<tr><td>Structure of theGU</td><td>markers of cessation of growth</td><td>scales and short internodes</td><td colspan="3">small leaves or aborted lamina</td><td>—</td></tr>
<tr><td rowspan="2">Branching</td><td>type</td><td colspan="2">rhythmic</td><td colspan="2">rhythmic to continuous</td><td>unbranched</td></tr>
<tr><td>chronology</td><td>immediate</td><td>deferred</td><td colspan="2">immediate</td><td>—</td></tr>
<tr><td>Leaves</td><td>phyllotaxy</td><td>2/5 spiral</td><td colspan="3">alternate distichous</td><td>—</td></tr>
<tr><td>Flowering</td><td>type</td><td>sterile</td><td colspan="3">short flowering branchlets</td><td>flower bearing</td></tr>
</table>

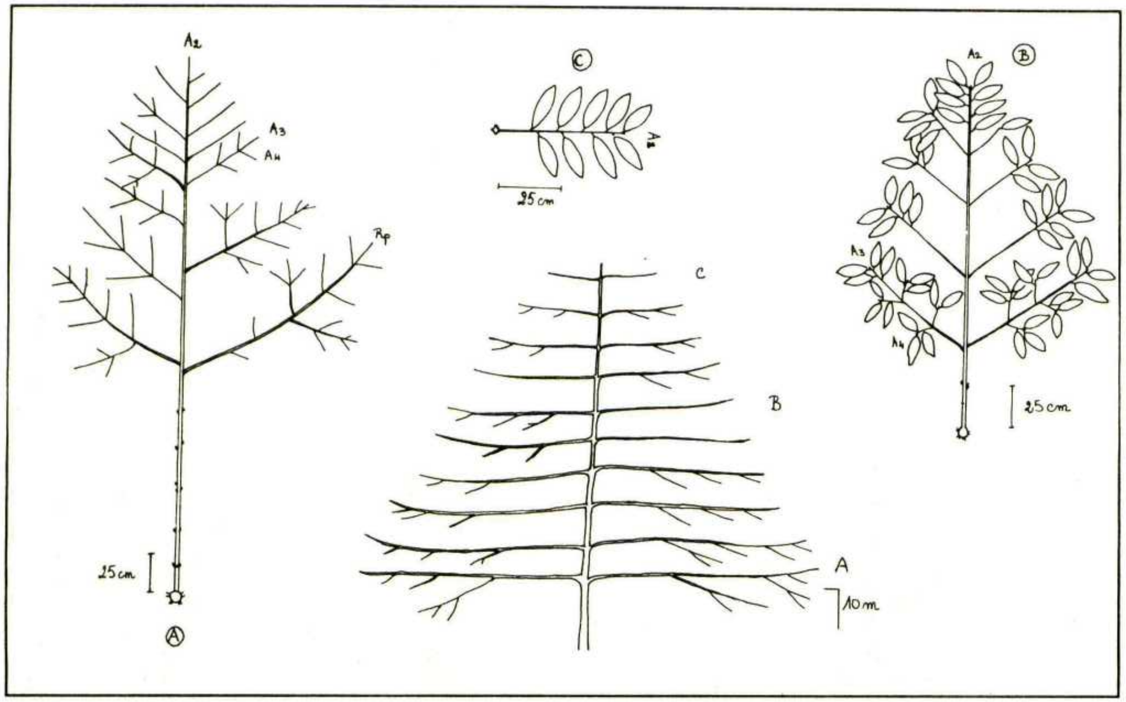


Plate 12. *Knema attenuata*: expression of the architectural unit.

Knema attenuata is dioecious (Pl. 13). The architecture of male and female trees is similar and can be differentiated only at the time of flowering and fruiting. Flowering is more abundant on twigs than on branches and branchlets. Some twigs seem to be "specialised", producing spurs at each node, and are smaller in size. There are more short branches and flowers in male plants (Pl. 13.1 & 2) than in female plants. Most of these short flowering branchlets are produced from the basal part of the GU.

Inflorescence is monopodial. The male spurs may bear 5-6 flowers each (Pl. 13.1b) whereas the female spurs generally bear 1-3 flowers each. The fruit is ovoid, tomentose and "apricot" coloured, about 2x4 cm in size with a bright red aril.

The adult tree

Once the tree has expressed its architectural unit, it produces reiterated complexes. The lower branches of the tree reiterate in a partial and sylleptic manner or fork (after the death of the apex), which enables it to spread out. Sometimes they also have total reiterations in their basal part.

The middle branches, with partial reiterated complexes, may get broken in the apical part and two kinds of reiterations can take place:

- total reiterations immediately after the break; their direction of growth may be vertical ("coat-hanger" branch) or oblique;
- partial reiterations with horizontal, oblique or vertical growth occupying maximum space through a large number of duplications, but conserving their distichous phyllotaxy (the distal part has a tendency to get repositioned horizontally).

The branches in the upper part of the crown are now exposed to sunlight and grow obliquely but remain plagiotropic. No changes was observed in the phyllotaxy of these branches. The structure of the trunk (axial symmetry) can be clearly distinguished from the structure of the branch (bilateral symmetry).

Total reiterations continue to be produced on the trunk only below the first basal branch and form the basal part of the crown. The tree gradually loses its structural regularity.

The tree of the past: senescence

The reiteration phenomenon becomes more pronounced with age. In their apical part, the biggest branches can produce total reiterations with oblique growth, as an extension of branches. The third order axes in the basal part of the branches get self-pruned little by little, leaving only the second order axis of the total reiterated

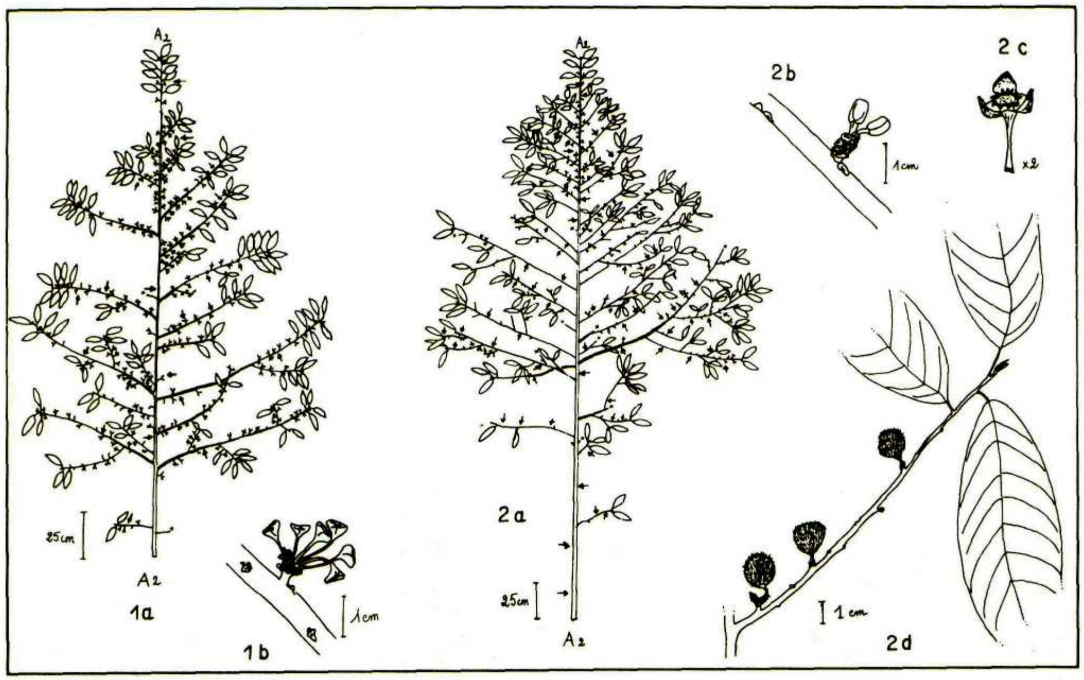


Plate 13. *Knema attenuata*: **1a** - Male branch. Position of the spurs; **1b** - Male flowering spurs;
2a - Female branch. Position of spurs; **2b** - Female spur; **2c** - Female flower; **2d** - Fruiting branch.

complexes, which then take on the role of twigs of the main branch. Total vertical reiterated complexes on this horizontal to oblique reiterated part are observed. The branch seems to grow by the addition of these reiterated complexes. The same phenomenon is observed with partial reiterated complexes which replicate the initial branch (bilateral symmetry). Some trees produce numerous total reiterations on the trunk (Pl. 14) which are big and form new main axes. The initial tree thus becomes a colony of smaller units.

The crown expands further and loses its regular structure due to the different reiterations. Flowering is profuse on these new reiterations along the large second and third order axes. Flowers are found at the periphery of the tree, whereas earlier they were within the crown.

At this stage, the tree does not grow in height any more and the top is made up of numerous total or partial reiterated complexes. On ageing, *Knema attenuata* produces more total and partial reiterated complexes in an irregular manner. The older trees thus have a non structured aspect, in contrast to the very regular structure of the younger ones.

Summary of the architectural development

From the first growth units, *Knema attenuata* puts forth some plagiotropic branches (Pl. 14.1). It conforms to Massart's model. The tree rapidly branches (Pl. 14.2). Twigs and branchlets and then flowering expressed by the emergence of spurs compose the architectural unit.

Once all the types of axes are developed, the tree begins to reiterate totally below the first branch of the crown (Pl. 14.3). The phenomenon of reiteration becomes more important and it is observed that, in the shade, adult trees develop more total reiterations in the lower part of the crown (Pl. 14.4a). *Knema attenuata* favours partial reiteration (Pl. 14.4b) when there is more light.

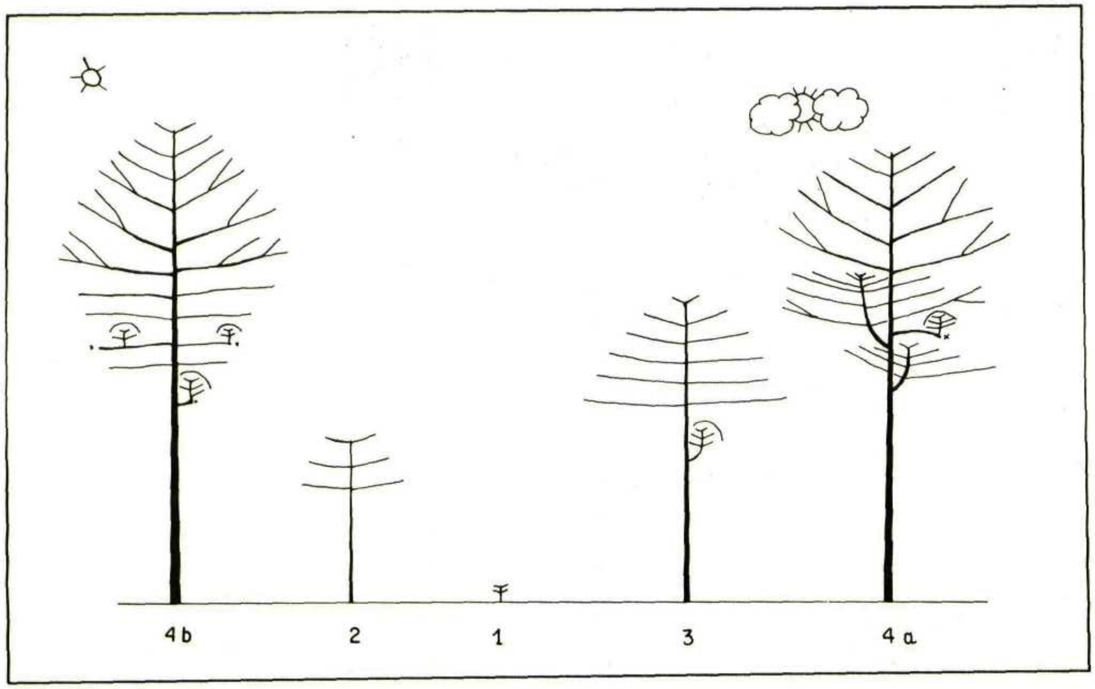


Plate 14. *Knema attenuata*: scheme of development.

Discussion

Architectural analysis enables the characterisation of the "average" tree which represents the "expression of an equilibrium between endogenous growth processes and external constraints exerted by the environment" (Edelin 1984). In the forest, competition among plants (for water, nutrients, space and light according to the forest structure and their location in the forest) induces the plants to evolve different growth strategies. *Vateria indica* and *Knema attenuata* both conform to Massart's model but exhibit different ways of building up their crown and different strategies of reiteration. How do the trees grow "towards light"? Which are the structures developed by the species to maintain their growth under the canopy? How are they regulated according to tree height and to the availability of light? Such questions are dealt with below.

Set-up of the architectural unit

In the undergrowth, light availability is low up to a height of about 5-6 m. From the first growth units on the trunk, the young plants of *K. attenuata* begin to produce branches. Growth units on the trunk have very few leaves (only at the last nodes), whereas the photosynthetic activity of the plant is ensured by the branches which bear leaves on nearly all their nodes. In contrast, young *V. indica* trees produce branches only after a minimum of 10 GUs. Their growth is slow and apical mortality is common (Durand *et al.* 1995). Scales, indicating waiting period, are often found on the trunk. Although the number of leaves per growth unit does not exceed 6, they are large (about 25 cm long and 7 cm wide). Once branching is well established (tree of 5-10 m), very few leaves are retained.

K. attenuata, since its very first GU, quickly puts forth the different types of axis. This species rapidly invests in branching and builds a regular and complete structure while *V. indica* takes a very long time to establish its different axes. In the undergrowth, *V. indica* is "in waiting", with slow growth and frequent bud mortality; series of scales and small short lived orthotropic structures are produced for photosynthesis, representing only a temporary reprieve.

Both these species conform to Massart's model: they have one orthotropic trunk and plagiotropic branches. The plagiotropic habit of *V. indica* is exposed by the fact that their leaves, spirally arranged with a 2/5 phyllotaxy, are turned horizontally by a twisting of the pulvinus. Branches of *K. attenuata* are horizontal with alternate and distichous leaves.

As *K. attenuata* produces all its axes very quickly, the establishment of the architectural unit including flowering is well-defined. In contrast, *V. indica* shows different types of axes corresponding to its architectural unit —obligatory stage in their growth—, but these units are quickly modified through metamorphosis (all become orthotropic axes; see the basic structure of metamorphosis) and then flower. Once exposed to light, this basic structure is the main unit which extends and grows rapidly.

Reiteration pattern

During their growth, the two species need to replicate their architectural unit totally or partially. Between 10 and 15 metres, plants invade the available space with several strategies. Young *K. attenuata* trees partially duplicate the structure of the branches in the lower part of the crown. The lower branches of *V. indica,* where apical mortality is frequent, put forth 3 "relays" which grow in 3 different directions enabling the plant to explore more space. Up to 15-20 m, *K. attenuata* reinforces its structure through partial reiterations and forking, and at the base of the crown through total reiterations from the trunk. *V. indica* occupies the available space, opens its crown by metamorphosis and by replication of the basic structure, reinforced by partial reiteration in the structure, forming crownlets.

Other types of reiteration are produced in order to increase the photosynthetic activity. The amount of light does not seem to be sufficient between 10 and 15 metres. *K. attenuata* produces one or more total reiterated complexes on the trunk ("coat-hanger" branches; in the distal part or in the middle part of the branch (Edelin 1984)), while *V. indica* renews its small orthotropic structures. Up to 15-20 m, *K. attenuata* reinforces the base of the crown through total reiterations from the trunk. It produces flowering branches even before reaching the canopy. *K. attenuata,* having already ensured flowering, produces vertical and horizontal reiterations (total and partial) in order to lengthen its branches. *V. indica* produces some total reiterations on the branches and sometimes on the trunk but only if growth is hampered (pollarded tree, blocking by other trees, *etc.)*

Tree competition

Before reaching the canopy, the trees may be hindered by a taller neighbour tree. For *V. indica,* the stem of such small trees starts bending and the apex of the trunk eventually dies. These trees then produce total vertical reiterations from the basal part of the unbent trunk and the tree can once again resume its growth in height.

Older trees develop new structures to overcome the obstacle and put forth vertical total reiterations from the trunk and main branches. However, this phenomenon is rare and occurs only when light becomes a critical factor for the crown. Thus, *V. indica* continues to grow towards the canopy by the addition of these different reiterated complexes, In contrast, *K. attenuata* can produce some total reiterations but usually cannot dominate the taller trees. For these total reiterations, it depends on the available space and light.

Role of light availability

Tree architecture can thus change according to light resources and to the presence of other trees in the forest structure. In most cases, light in the undergrowth is not uniform and young trees with just one metamorphosed branch are often observed.

V. indica is a species which reacts to light, especially when the tree metamorphoses. Once the entire crown is exposed to light (at the canopy level), *V. indica* metamorphoses throughout its crown and flowering begins. The reiteration phenomenon thus becomes increasingly important. Its structure is then hierarchically organized. At the canopy level, *V. indica* extends its crown by the addition of different forms of reiteration (sylleptic and proleptic) and becomes polyarchic (Edelin 1991), forming independent crownlets. Small vertical reiterations are produced before the branching part of the main branches. These structures are relatively short lived, and like the orthotropic structures in young trees, participate temporarily in photosynthesis.

In contrast, with the increase of light availability, the structure of *K. attenuata* becomes disorderly and irregular through the addition of some vertical partial reiterated complexes in the apical part of the branches. Once the canopy is reached, *K. attenuata* seems to be poorly adapted architecturally and its structure becomes disordered: the species loses its earlier regular architecture.

Conclusion and perspectives

In the initial stages, *Knema attenuata* has a regular structure. It gradually strengthens it in order to occupy the maximum possible space. The regularity and density of its structure is its strength. This species flowers even before reaching the canopy, thus ensuring its perenniality. However, the inability of *K. attenuata* to adapt itself to obstructions at the canopy level, leads to it losing its rectilinear structure. The light factor thus seems to destroy the initial regularity and the tree continues its growth by the addition of structures which are not very stable (short life span and sprouting in all directions). Therefore, *K. attenuata* maintains its position of a lower canopy tree through its very regular structure until it reaches the canopy and then tries to further its growth. *K. attenuata* has a very hierarchic structure from its youngest stage.

At the beginning, *Vateria indica* presents a fairly slender structure in the undergrowth but has the structural means to renew it and maintain its growth. As soon as there is enough light, it begins to metamorphose and the structure gets increasingly reinforced. It establishes its vertical structure and then grows horizontally, ensuring its position as an emergent. Soon after, flowering begins. *V. indica* is a plastic species which can adapt very well to different environmental conditions thanks to its efficient capacity to reiterate. Under poor light condition, *V. indica* has a delayed and poor hierarchic structure and its architectural unit is fugacious and not well-defined. When light is no longer a limiting factor, the metamorphosis of axes allows *V. indica* to change its architectural organisation and become hierarchic, to reach the canopy and occupy the available space.

It is intended to conduct a similar study on two other species which are also common in the Kadamakal Reserved Forest and play contrasting roles in forest dynamics and structure: an emergent, *Dipterocarpus indicus* (Dipterocarpaceae), whose strategy can be compared to that of *Vateria indica;* and an understorey species, *Humboldtia brunonis* (Fabaceae). The different aspects of phenology will be treated (desynchronism between trunk and branches, sexuality, *etc.).*

A more detailed quantitative study will be conducted on the relationship between tree architecture and the availability of light in the understorey: diverse situations of forest structure (Pélissier 1995) will thus be investigated. A less detailed study on the architecture of several other common species will also be undertaken. The relationship with secondary growth is already being studied in order to assess whether and how it depends on light availability, on the stage of architectural development and on the vertical position of the trees in the forest.

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